

LIFE HISTORY AND IMMATURE STAGES OF
PARYDRA BREVICEPS (DIPTERA: EPHYDRIDAE)

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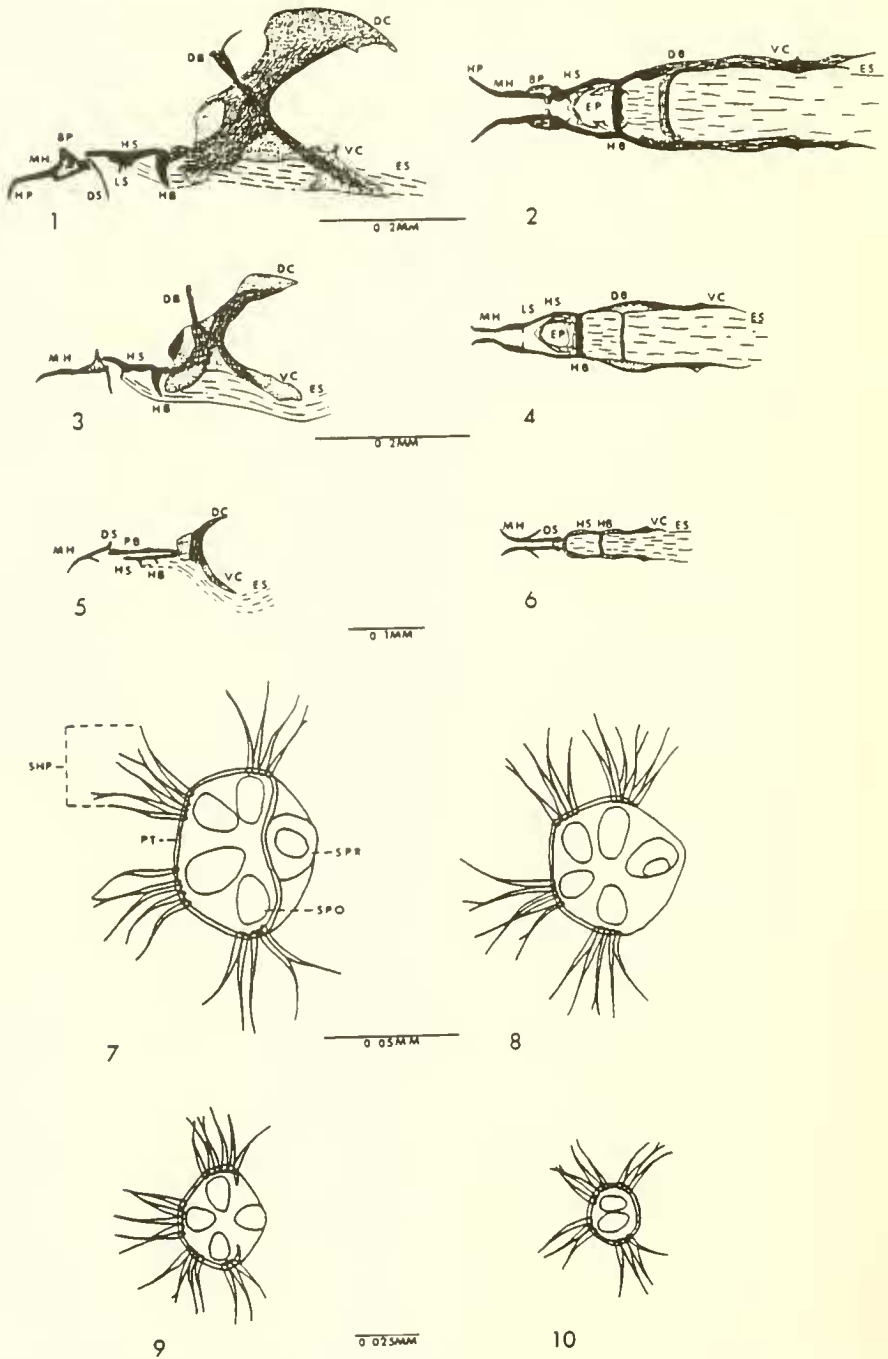
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Abstract.—Adults of *Parydra breviceps* Loew occur most abundantly on mud shores, where they feed mainly on benthic diatoms. Eggs are laid on emergent objects on the mud shores in masses of mostly 1–2 eggs. Eggs are covered by a thin, uniform, light-green fecal layer, which turns white in old egg masses. Development from egg to adult requires between 14–17 days at temperatures of 20–26°C. The eggs start to hatch after 3–4 days. Each of the three larval instars lasts 3 days in most cases and 4 days in some others. The puparial phase lasts 2–3 days. Pupariation occurs on or above the mud surface, in thin layers of mud covering rocks, or in mud at the base of plants. Collecting shows the adult over-winters at moderate latitudes (puparia probably also over-winter). Some gravid females were collected in winter. Adults collected in late October, November, and December had guts packed with diatoms. Dissections of field-collected specimens showed that diatoms outnumber any other algae found in the guts of *Parydra breviceps*. The egg, three larval instars, and puparium are described and illustrated. Comparisons are made with *Parydra aquila* and *P. quadrituberculata*.

Shore flies, or Ephydriidae, now numbering over 1200 species, constitute important and ubiquitous components of inland littoral and wetlands communities as well as many marine coastal communities. In all of these situations, the adults live above the water while the larvae live in water, wet mud or sand, and algal mats where they feed upon various algae and microbes. Larval habits and microhabitats of many diverse types have been reported (Becker, 1926; Bohart and Gressitt, 1951; Deonier, 1971; Thorpe, 1930; Wirth, 1971).

Information on the life history and immature stages of Ephydriidae is restricted to less than 10–15 percent of the nearctic fauna. Deonier and Regensburg (1978) reported on the biology and immature stages of *Parydra quadrituberculata* Loew. Thier and Foote (1980) compared ecological data for 11 species of mud-shore Ephydriidae in northeastern Ohio.

Our studies on *Parydra breviceps* Loew were conducted during the period 1979–81 at three main sites: Site 1—Brandywine Co., 0.8 km S. of Bath, Franklin Co., Indiana. Pastureland, springfed brook with average water depth of 30 cm. Site 2—Harkers Run, 1.5 km E. of Oxford, Butler Co., Ohio. Woodland stream with narrow mud shore on 45° shore slope with water depth of 20–50 cm. Site 3—Four-mile Cr., 300 m. SW of site 2. Extensive 5 × 5 m mud flat surrounded by grasses and woodland shrubs.



Figs. 1-10. *Parydra breviceps*. 1, Third-instar larva, cephalopharyngeal skeleton, lateral view. 2, Same, ventral view. 3, Second-instar larva, cephalopharyngeal skeleton, lateral view. 4, Same, ventral view. 5, First-instar larva, cephalopharyngeal skeleton, lateral view. 6, Same, ventral view. 7, Pupa, left posterior spiracle, distal view. 8, Third-instar larva, left posterior spiracle, distal view. 9, Second-instar larva, left posterior spiracle, distal view. 10, First-instar larva, left posterior spiracle, distal view.

Voucher specimens from the study are in the Miami University Insect Collection.

Abbreviations used in illustrations are: AN, anus; ASP, anterior spiracle; BP, basal part of mouthhook; DB, dorsal bridge; DC, dorsal cornu; DCC, dorsocephalic cap; DS, dental sclerite; EP, epistomal plate; ES, esophagus; HB, hypostomal bridge; HP, hook part of mouthhook; HS, hypostomal sclerite; LS, ligulate sclerite; LPT, lateral postanal tubercle; MH, mouthhook; PA, papilla, PAE, postanal elongation; PAP, perianal pad; PSP, posterior spiracle; PT, spiracular peritreme; SA, spiracular atrium; SHP, spiracular hydrofuge process; SPO, spiracular orifice; SPR, spiracular remnant (scar); TS, tracheospiracular siphon; VC, ventral cornu; VPT, ventral postanal tubercle.

LIFE HISTORY

Of the 34 nearctic species in the cosmopolitan genus *Parydra* (Clausen and Cook, 1971), *P. breviceps* is considered to be third in abundance in its distribution range (30°–50° latitude in North America) after *P. quadrituberculata* and *P. aquila* (Fallen).

Adult.—Adults of *P. breviceps* are semiglossy dark brown flies, with a bulging, light-gray pruinose face (Fig. 11). They lack the paired incurved spines on the probasisternum and the 2 pruinose areas on the mid tibiae found in *P. quadrituberculata* (Deonier and Regensburg, 1978). The males are 2.6–3.0 mm long and the females 2.8–3.6 mm.

The feeding apparatus of *breviceps* consists of highly modified labellar canaliculi (pseudotracheae), which are arranged in 6 or 7 pairs of fanlike processes attached to the paired distal labial palpal sclerites and a medial horseshoe-shaped sclerite. Frey (1921) calls that sclerite the middle part of the furca. The length of rays increases anteroposteriorly up to the second to last fanlike canalicular process. The rays in the last fanlike canalicular process (posterior direction) are slightly smaller than the preceding rays.

As in the study by Deonier and Regensburg (1978), evidence in this research shows that the fanlike canalicular processes in *breviceps* serve for sifting and scooping of diatoms, some unicellular green algae (*Closterium* sp., *Cosmarium* sp.), and detritus. *Navicula* spp. were the most common diatoms in gut dissections in the feeding areas of the mud shore habitats. However, on many occasions segments of *Oscillatoria* sp. and *Melosira* sp. were found in the guts of *breviceps* (Fig. 12) and *quadrituberculata*, which could indicate that they are able to rasp off segments of some algal filaments. During feeding the canalicular processes are spread into the ooze. As in *quadrituberculata*, when feeding (not drinking), the haustellum is flexed rapidly, but incompletely, while the canalicular processes fold in and out. The food particles are carried on the canalicular processes to the central prestomum. When *quadrituberculata* and *breviceps* were taking up fluid for example from a water droplet, no movement of the haustellum or canalicular processes was observed.

Dissections of the gut revealed that the entire gut of *breviceps* is similar anatomically to the gut of *quadrituberculata*. Quantitatively, the filling of the different parts of the gut often depended on the time of the day. Early in the morning some peritrophic envelopes were empty, some showed partial filling in the middle and hindgut or just in the hindgut. Fig. 12 shows the gut contents of a female *breviceps*,

containing many diatoms, some detritus, *Closterium* sp., and *Oscillatoria* sp. In most cases when the guts showed some filling, they contained detritus or sand particles, and in many instances the detritus constituted 50–90 percent of the gut contents.

Qualitatively, the composition of the crop and midgut contents appeared similar. In this work, it was found that the membrane was distinctly visible in fresh or in preserved adults especially if it enclosed food particles. The peritrophic envelope was so distinctly visible because of a space between it and the gut wall. Furthermore, the membrane (envelope) became clearly visible because in the fall it turned light red in many of the older *quadrituberculata* and *breviceps* collected in the field. In dissections, the peritrophic envelope could easily be pulled out of sections of the gut (Fig. 12). Dissections showed that *breviceps* has the anterior and posterior spinulose plates of the rectal valve which could account for peritrophic envelope transport and fragmentation.

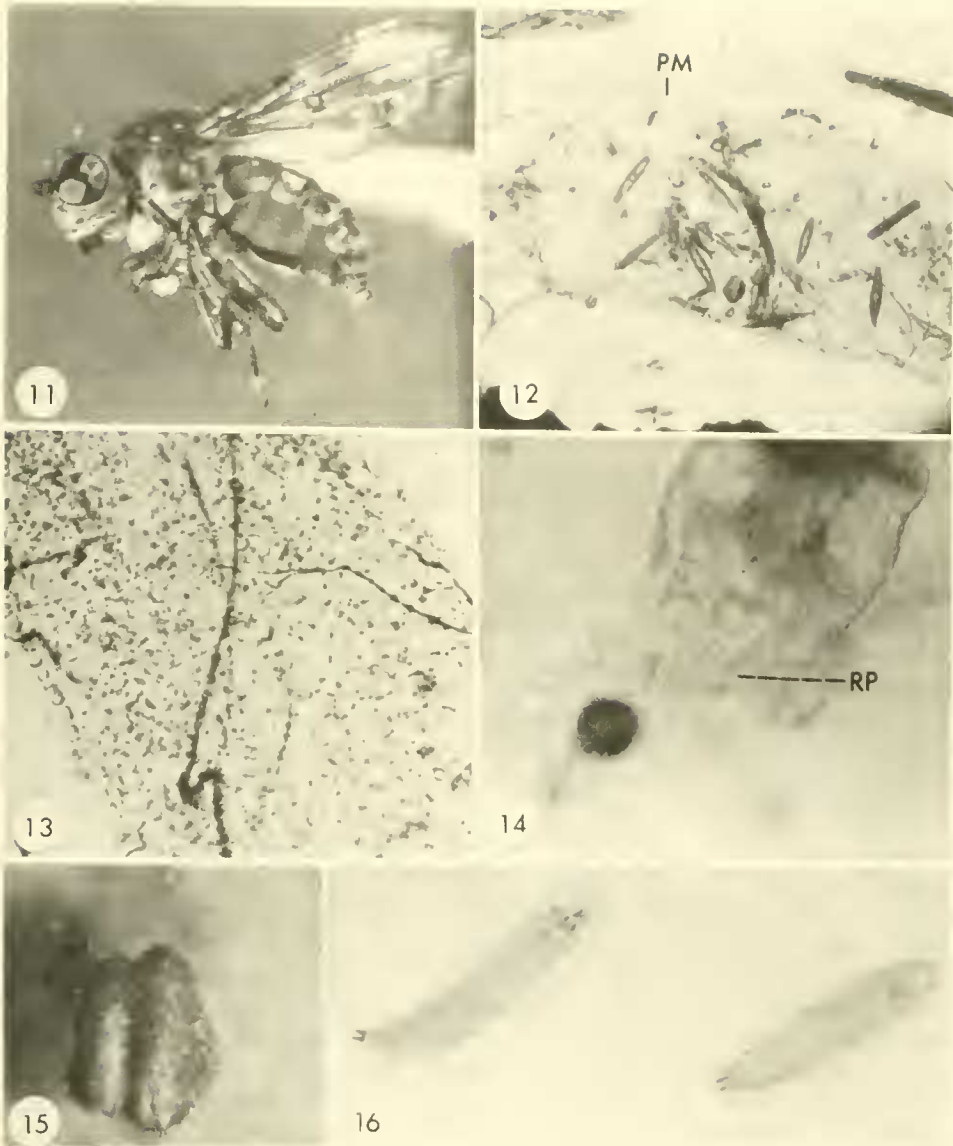
The following daily activity rhythm was observed during 24-hour sampling and observation periods and during the periodic field collecting. The daily activity rhythm on mostly sunny days, with temperatures above 20°C, was different from rainy or cold days.

During darkness adults of *aquila*, *breviceps*, and *quadrituberculata* were observed roosting almost exclusively on green vegetation immediately next to or on the mud shore where they fed. Adults of these three species were often intermixed and as close as 1 or 2 mm from each other on a grass blade. The arrangement was most often head to tail and headed upward beginning at a few mm to about a meter above the mud.

No feeding was observed during darkness but the onset of light did not seem to be a stimulus or the only stimulus for the *Parydra* to start feeding. Even after sunrise and at temperatures around 12°C, adults were not seen feeding. However, it was observed that in these early morning light hours the roosting adults were much more easily disturbed and stimulated to fly to another roosting site. We noticed that when at or after sunrise the air temperature rose to about 16°C, the number of feeding adults increased even if the sky was overcast. The number of roosting adults decreased during the same period. During the day very few adults of *breviceps* or *quadrituberculata* were seen at the night roosts.

Daytime activities consisted mostly of periods of feeding alternated with periods of cleaning and resting. Between these activities copulation and oviposition were also observed. Copulation attempts were not observed in the night roosting sites, but only during the feeding, cleaning, or resting periods in the feeding area.

During the feeding, or grazing period, which generally started about noon, the flies moved over the substrate tapping it at various spots with one or both fore tarsi, but more often with the proboscis in search for food. In tanks with substrate low in diatoms, the adults of *breviceps* moved around and probed the substrate with their proboscises in various spots much more often and fed less than the same insects on mud rich in diatoms. When small spots of substrate rich in diatoms were placed in tanks with substrate poor in diatoms, *quadrituberculata* and *breviceps* often flew directly to these spots or found them very quickly by probing on the substrate. Analysis of substrate samples from the field showed that most adults fed on a mud shore at the places where the food density was highest. The adult found an adequate feeding spot by moving and probing the substrate with the



Figs. 11–16. *Parydra breviceps*. 11, Female, gravid, 19 \times . 12, Female, content of peritrophic envelope [membrane] (diatom spp., *Oscillatoria* sp., *Closterium* sp.), 300 \times . 13, Male, gut containing oil droplets, 300 \times . 14, Adult, rectal valve with rectal plates, 300 \times . 15, Two eggs with fecal covering and opened micropyle, 45 \times . 16, Two first-instar larvae, dorsal view, right larva retracted, 45 \times .

proboscis. When this spot was found, it started feeding with minute anteroposterior oscillations of the proboscis and larger lateral movements of the whole head, leaving a zig-zag feeding track on the diatom-rich substrate. The feeding activity of *quadrituberculata* and *breviceps* was often accompanied by dipping movements of the abdomen. Defecation occurred during feeding and when the abdomen was characteristically dipped. Fresh feces, which were released on the substrate while

feeding, had a very dark brown color, whereas the feces in the roosting sites looked more like the egg covering.

During the feeding period the proboscis was periodically retracted for about 1 sec and then feeding resumed. The anteroposterior oscillations of the proboscis and abdominal dipping movements were observed only when the insects were feeding on substrate. When the same insects were observed taking up fluid from wet filter paper or from a water droplet, no oscillations of the proboscis or dipping movements of the abdomen were observed.

Grooming or cleaning often occurred after *breviceps* moved to a new feeding spot and after a disturbance. Grooming in *breviceps* consisted of rubbing the hindlegs (tibiae and tarsi) along the wings, rubbing mid- and hindlegs together, rubbing hindlegs against each other, rubbing hindlegs over abdomen, thorax, and even the eyes, forelegs rubbing against each other and fore tarsi cleaning eyes, face, and genae. Disturbances in the roosting site at night and at the resting sites during the day often initiated this cleaning activity. Mating, which was observed to take place during feeding activity, was also very often succeeded by grooming.

In *breviceps* no courtship posturing was observed in the field or in the laboratory. Copulation was only observed when the female was feeding. The male either flew towards the female, landing on the substrate about 5 cm away from the female, and then just leaped on the female, most often from behind, or the male approached the female while both were feeding and after some hesitation, stopped feeding and jumped the female from behind from 1 to 3 cm distance. In *breviceps*, in about three out of ten trials in which mounting was not successful, the female shook the male off before copulation could take place. Sometimes the male was successful with its second or third try. It appeared that females did not allow any immediate subsequent mounting after copulation took place. During copulation in *quadrituberculata* the male grasped the female with his fore tarsi at the basal costal area of each wing and separated the wings of the female with its hind tarsi. The male grasped the abdomen of the female with the mid and hind tarsi. The male assumed an angle of approximately 60 degrees with the longitudinal axis of the female. During mounting and copulation the female continued feeding and moving around on the substrate. Copulation lasted from just a few seconds to more than a minute. In the post-insemination phase of *breviceps*, dismounting appeared to be initiated by the female flexing her wings, trying to brush off the male with her hindlegs, and by vigorously moving her abdomen.

Besides feeding and grooming, *breviceps* also showed resting behavior. After feeding for several minutes or after grooming, the flies often moved to a rock, fallen leaf, or another piece of vegetation in the feeding area, or often just stayed on the mud and remained motionless for up to 30 min. Sometimes grooming was also observed during these daytime resting periods. Generally the daytime resting periods of *breviceps* and *quadrituberculata* were within the feeding area. The insects were also much more alert during their resting periods than during the roosting periods.

Data show that *breviceps* is more abundant in narrow mud shores with interspersed or closeby vegetation. No *breviceps* were ever collected in an artificially created mud flat along a narrow mud shore which otherwise had a small, relatively constant population of the species.

Oviposition and fecundity.—In laboratory-reared *breviceps*, mating occurred

within 1 to 3 days after emergence. The first eggs were laid 4–5 days after emergence and egg laying continued for 8–14 days. In field-collected *breviceps*, mating and oviposition could be observed in the laboratory the same day the insects were collected.

A maximum of 115 eggs and developing eggs were found in a dissected specimen of *breviceps* which was reared in the laboratory. A female of *breviceps* collected in the teneral stage at East Fork of Four Mile Creek in Hueston Woods State Park, Ohio, laid 226 eggs within 16 days. One hundred and sixty-four eggs were deposited in groups of two and 62 singly. Females reared in the laboratory laid between 33 and 220 eggs. The first eggs laid were mostly deposited singly. Most eggs were usually deposited in groups of two (Fig. 15), rarely in groups of three.

Oviposition was most often observed from midafternoon till roosting time. In the field, eggs of *breviceps* were found side by side with eggs of *aquila* and *quadrituberculata*. Eggs were most often deposited on objects within the feeding area. Fewer eggs were found at the roosting sites. Eggs were mainly deposited on rocks, pieces of glass, pieces of metal, fallen leaves, pieces of wood and on vegetation growing in or adjacent to the feeding area and as high as 2 m above the water level.

In the laboratory, if *aquila*, *breviceps*, and *quadrituberculata* were reared in the same tank, eggs of the three species were deposited side by side. In the holding tanks the three species laid their eggs on rocks, pieces of wood, dead or growing vegetation, and on the glass walls of the tank. If there was only mud in the tank, all eggs were deposited on the glass walls of the tank. Most eggs on any substrate, whether rock, vegetation or glass, were deposited only millimeters above the mud. No eggs were deposited on the mud or on dry sand. When the female of *breviceps* had selected her ovisite, she often remained there motionless for sometimes 1 minute before ovipositing. Prior to and during oviposition, there was a very slight dipping movement of the abdomen. The eggs adhered to the substrate and immediately after ovipositing the female covered the eggs with a green layer of feces consisting of variable proportions of empty and broken diatom frustules, mixed with light-green pigments.

Development.—In the laboratory, development from egg to adult lasted 14–17 days in 13 different holding tanks and 12 Petri dishes at temperatures from 20–26°C. The 25 females of *breviceps* used in this experiment laid a total of 1300 eggs, from which 777 larvae eclosed after an incubation period of 3–4 days. Each of the three larval instars lasted 3–4 days and the puparial phase lasted 2–3 days. A total of 364 puparia were counted. About 210 adults of *breviceps* emerged from these puparia. At the temperature of 30°C, development from egg to adult lasted 21–22 days in five different holding tanks and 9 Petri dishes. The eggs hatched after about 4 days, each larval instar lasted between 3–5 days, and the puparial phase lasted 2–4 days. At 30°C very few eggs developed to puparia or adults. The females of *breviceps* laid an average of 52 eggs in this experiment. In four of the five holding tanks only about 2 out of 52 eggs completed development to the adult stage.

In another experiment, two virgin males and two virgin females of *P. breviceps* and of *quadrituberculata* were placed in one holding tank with diatom-rich substrate. The females of *breviceps* laid an average of 96 eggs, whereas the females of *quadrituberculata* laid an average of 404 eggs. The first *quadrituberculata* emerged

14 days after the first oviposition was observed and the first *breviceps* 16 days after the first oviposition. Emergences in both species continued for 27 days. In the first part of the emergence period the *P. quadrituberculata* were much more numerous until the latter part of the period when emergences of *breviceps* became more numerous. A total of 70 *quadrituberculata* and 18 *breviceps* emerged. Therefore, in *quadrituberculata* 8.6 percent of the eggs developed to the adult instar whereas in *breviceps* 9.5 percent of the eggs developed to adult instar.

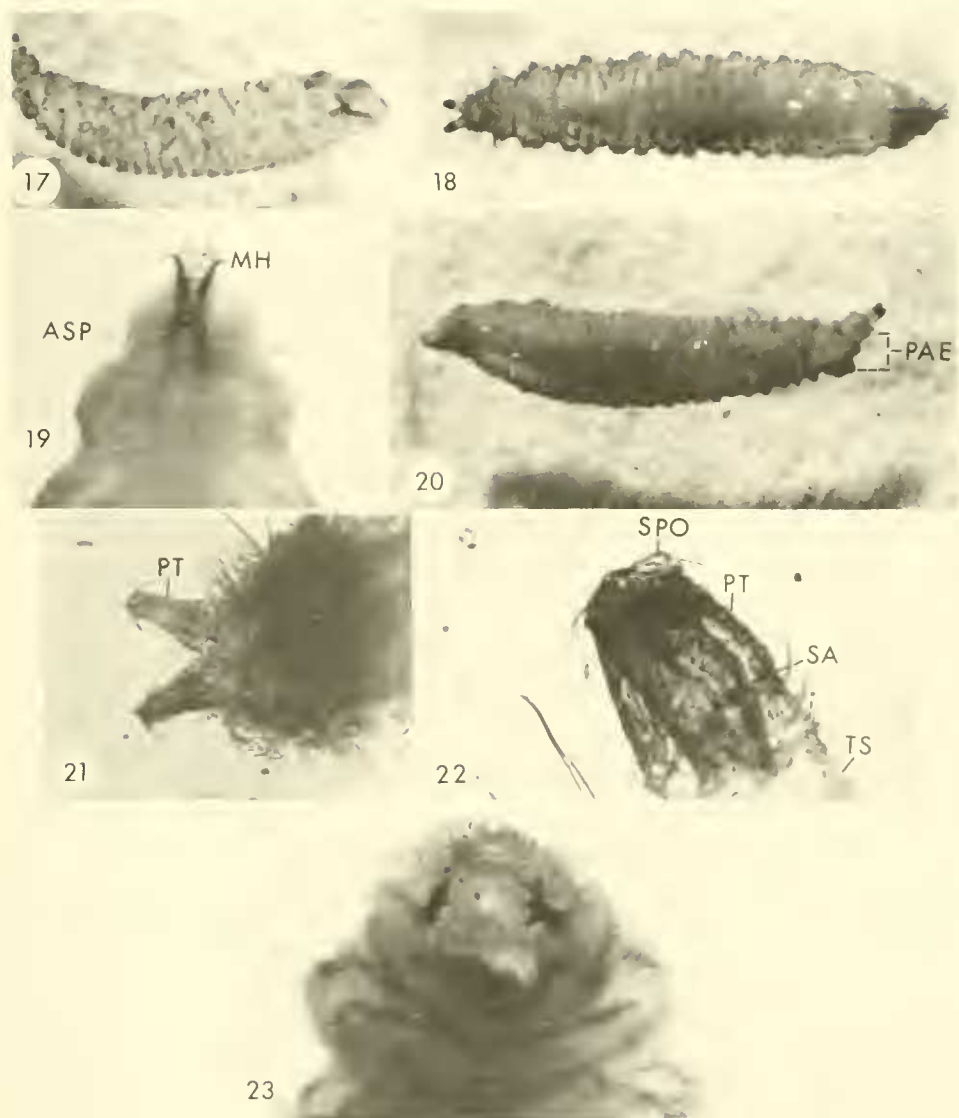
Larva.—Very few larvae of *breviceps* were collected in the field. In an attempt to determine where larvae of *breviceps* occur in their natural habitat, 15 first-, second-, and third-instar larvae were released on mud shores where adults had been seen feeding. The general tendency was to move downward on a slope. When the larvae reached a little depression in the mud they burrowed into the substrate.

In the laboratory, it was found that larvae of *quadrituberculata* and *breviceps* moved toward a good food source without being in direct contact with it. When fresh diatom-rich substrate was added to the diatom-poor substrate present in the tank, within 15 to 30 minutes most larvae were found in the small area of diatom-rich substrate on one end of the tank. When the new substrate was added, some larvae were as far as 30 cm away from the new food source.

Deonier (1972) and Deonier and Regensburg (1978) reported that diatoms constituted the vast bulk of the gut contents in adults of *quadrituberculata* and that the guts of the larvae were packed with diatoms. Thier and Foote (1980) found diatoms and a small quantity of *Oscillatoria* sp. (as the only non-diatom algal genus) in field-collected larvae of *aquila* and *quadrituberculata*. In this study, besides the main constituents of diatoms, frequently *Oscillatoria* sp., *Closterium* sp., and *Cosmarium* sp. were found in larval and adult guts.

Thier and Foote (1980) indicated that food particle size could be a mechanism segregating *Parydra* species. Experiments in the present study also showed that food particle size is important. Larvae of *breviceps* that were placed on plates containing diatoms of 0.02 mm length or more died after a few days. Dissection of the guts showed that they were either empty or that they contained only a few of the rare smaller diatoms occurring on those plates. Larvae of *breviceps* could feed and develop only when placed on plates containing mainly diatoms of 0.014 mm maximum length. However, larvae of *quadrituberculata*, even first instar, were found to be able to feed on diatoms of 0.02 mm, 0.03 mm, and larger lengths. This could be a major determinant of overall abundance of the two species. Larvae of *breviceps* could be successfully raised in holding tanks on diatom-rich substrate, because those diatoms were scraped from rocks in flowing water in order to obtain many smaller-sized diatoms.

In dissections of adults and larvae there was generally a striking difference in the amount of sand particles or detritus found in the gut and also in the degree of fragmentation of the diatoms. We believe that these two facts are interrelated. In the adult, quite often when the number of diatoms on the substrate was low a large part of the gut content was detritus. As already mentioned, one of the functions of the detritus could be to pack the gut and ensure diatom fragmentation through gut contractions, mostly in time of low diatom density. In the larvae, very little diatom fragmentation could be found in over 50 dissections of all three larval instars. Therefore, it can be assumed that detritus is not important in the larvae to help pack the gut to ensure diatom fragmentation.



Figs. 17-23. *Parydra breviceps*. 17, Second-instar larva, lateral view, 45 \times . 18, Second-instar larva, dorsal view, 45 \times . 19, Anterior end, ventral view of third-instar larva, 50 \times . 20, Third-instar larva, lateral view, 20 \times . 21, First-instar larva, posterior spiracles, lateral view, ventral view of larva, 300 \times . 22, Third-instar larva, posterior spiracle, lateral view, 300 \times . 23, Third-instar larva, headlobe retracted, anterior spiracles visible, 90 \times .

Pupariation.—In laboratory observations, larvae restricted their movements to the substrate they were feeding on until shortly before pupariation. One or two days before pupariation the third-instar larvae crawled on the covers of the Petri dishes and as high as 30 cm on the glass walls of holding tanks. To investigate if this larval movement was associated with food searching, control and experimental groups of 10 larvae each were individually placed on diatom-rich substrate

in Petri dishes. In the control group, the larvae fed on the same substrate for the duration of the experiment (7 days) but in the experimental group, fresh diatom-rich substrate was added every day to the Petri dish. No difference was observed in the two groups in larval movement from the substrate onto the Petri dish covers. Because this movement happened shortly before pupariation, it seemed obvious that the larvae were searching for a place to pupariate. *Parydra breviceps* were rarely observed pupariating in the flat substrate they fed on. If they pupariated in the mud, it was on elevated places where the mud was drier. When small mounds of fine, dry quartz sand were placed on the mud, no larvae chose those drier areas for pupariation. In the laboratory, most *breviceps* pupariated along the glass walls of holding tanks just a few millimeters above the mud or in thin layers of mud covering rocks, or in mud at the base of plants which was somewhat elevated. Even the puparia on the glass walls had a thin mud covering, carried up with the setulose integument of the third instar. If the mud around the puparium was allowed to dry out, the adult often did not emerge. When the holding tanks were covered with clear plastic to insure high air humidity on the inside, puparia could be found as high as 30 cm upon the glass walls.

This selection of shallow or superficial pupariation sites by larvae of *breviceps* is in contrast to the deeper sites in the mud substrate selected by larvae of *quadrituberculata*. Beginning in the third larval instar of these species, there is a complete reversal in the ratio of postanal to preanal length of the body, with the postanal being 13.5 and 10 percent of the preanal length respectively for *breviceps* and *quadrituberculata* in the second instar in contrast to 8.7 and 16.7 percent respectively in the third instar. This is vastly accentuated in the puparium which in *breviceps* has a short, relatively straight postanal region, or "respiratory tube" (13.7 percent of preanal length), but which in *quadrituberculata* has a postanal elongation 50+ percent of the preanal length and upturned.

Overwintering.—In the fall of 1979 and 1980, when the night temperatures dropped below freezing for several nights, the number of adult *aquila*, *breviceps*, and *quadrituberculata* observed in the feeding or roosting areas or collected with the aerial net dropped significantly. In October and November of both years when the day temperatures did not reach 10°C, no *Parydra* were collected in the feeding or roosting area with an aerial net. If the day temperatures were above 10°C, all three species were collected in low numbers (between 1 and 10 specimens per species per 100 sweeps) at sites 1 and 2. The relative number of *breviceps* increased, and as many or more *breviceps* than the other two species were collected at sites 1 and 2 in October and November of 1979 and 1980. *Parydra breviceps* collected at the end of October and in November showed increasingly higher numbers of diatoms in their guts. For example, on November 9 and December 8, 1980, when the air temperatures rose close to 20°C a total of 0 *aquila*, 11 *breviceps*, and 0 *quadrituberculata* were collected with an aerial net. The guts of these flies were heavily packed with diatoms, and contained some green pigments and practically no sand. The highest number of diatoms observed in *breviceps* all year was found in these specimens.

On January 17, 1980, with no snow on the ground, one gravid female *breviceps* was caught with the aerial net at site 1. The gravid female was taken to the laboratory and placed alone in a holding tank with diatom-covered mud. No eggs

were found in the tank until January 30. The female *breviceps* laid a total of 52 eggs and died 32 days after it was put in the holding tank. Nineteen days after the first eggs were found in the tank, the first emergences of 2 males and 2 females were observed and by March 5, 1980, a total of 12 males and 7 females had developed from the eggs of this overwintering female.

In February 1980, after a light snowfall and at ambient air temperatures of -7 to 0°C , a total of 3 males and 6 females of *breviceps* were collected with the shoreline flushing technique. In February 1980 and January 1981, substrate and vegetation samples brought into the laboratory from site 1 and site 2 and placed in holding tanks yielded 1 male and 3 females of *quadrituberculata* within a few hours. No larval activity, puparia or later emergences were observed in any of the samples. In February 1980, 5, and in February 1981, 2 solar-heated winter emergence traps were set up along Harkers Run and Four Mile Creek. Both years the traps were regularly checked until March 20, and they yielded a total of 1 *breviceps* and 6 *quadrituberculata*. Therefore, we conclude that *breviceps*, like *quadrituberculata*, overwinters as adults and perhaps as puparia in the study sites.

Mortality agents.—On May 23, 1980, a common toad bug, *Gelastocoris oculatus* Fabricius (Hemiptera: Gelastocoridae) was observed leaping on an adult of *quadrituberculata* and carrying it away. The prey and the predator were collected and the prey had a punctured thorax. However, in the laboratory no predation by toad bugs on *Parydra* could be observed. On June 3, 1980, 35 laboratory-reared *quadrituberculata* marked with red fluorescent spray paint on their wings were released in a natural habitat. The next day no marked *quadrituberculata* were seen alive, but 14 marked wings were found on the mud at the place of release.

Ochthera mantis (DeGeer) is a potential predator, but no predation by it on *breviceps* was observed in the field or in the holding tanks. *Ochthera mantis* were often seen side by side with *aquila*, *breviceps*, or *quadrituberculata* on the mud shores and while roosting.

On June 11, 1981, at 0400 hours a spider (*Schizocosa crassipes* Walckenaer) was observed in the light of a flashlight to leap on and kill a *quadrituberculata*. On June 18, 1981, at 0400 hours a spider (*Micrathena gracilis* Walckenaer) whose orb was in the roosting area of the *Parydra* was collected. The orb had a "food package" on it, containing 3 adults of *quadrituberculata*.

The fact that adults, larvae, and puparia of *Parydra* often aggregate, especially during drought conditions and also, as found in this work, in especially diatom-rich depressions within a mud shore, facilitates predation by shore birds. Deonier and Regensburg (1978) found numerous probing marks of killdeer in the ooze at Brandywine Creek. Reeder (1951) found adults and immatures of various Ephydriidae in the stomachs of certain salt-marsh feeding plovers and sandpipers. At site 1, killdeer (*Charadrius vociferus*) and common snipe (*Capella gallinago*) could often be seen feeding. Numerous probing marks in the ooze were found where adult *Parydra* could be seen feeding and where larvae of *Parydra* could be collected from the ooze.

Predation on *aquila*, *breviceps* or *quadrituberculata* eggs has not been observed in the field or in the laboratory. However, potential egg predators were often associated with the *Parydra* populations. Deonier and Regensburg (1978) stated that the fecal covering is an imperfect defense against egg parasitism. Thier et al.

(1976) reported rearing *Anaphes* sp. (Hymenoptera: Mymaridae) from eggs tentatively identified as *quadrituberculata*. Meyers (1981) found *Anaphes* sp. (Hymenoptera: Mymaridae) to be an egg parasite of *aquila* and *quadrituberculata*.

Parasitic mites have been found on *Hydrellia griseola* (Fallén) (Deonier, 1971) and, in the present study, these mites were found on adults of *aquila*, *breviceps*, and *quadrituberculata* from all three sites. In 1980, mites were found on field-collected *Parydra* from June 19 until September 13, when the number of *Parydra* decreased considerably. In 1981, parasitic mites were found in almost every field collection of *Parydra* from June 12 to July 23 when the number of adults decreased in the field.

Nematodes were found in the abdomen of field-collected adults of *aquila*, *breviceps* and *quadrituberculata*. In 1980, nematodes were found in field-collected *Parydra* from July 17 to October 10 and in 1981 from June 17 to August 22. Nematodes were often found in teneral of the three species.

Very few eggs, larvae, or puparia of *breviceps* were collected in the field. In the few specimens no egg, larval or puparial parasites could be detected. Meyers (1981) attempted to study the rates of parasitism for larval populations of *breviceps* and *quadrituberculata*. However, he could not find populations of immatures of *breviceps* in the field. Observations were made on *Kleidotoma* sp. (Hymenoptera: Eucoilidae) in the laboratory where the wasps could be observed to attack larvae of *quadrituberculata*, but not larvae of *breviceps*.

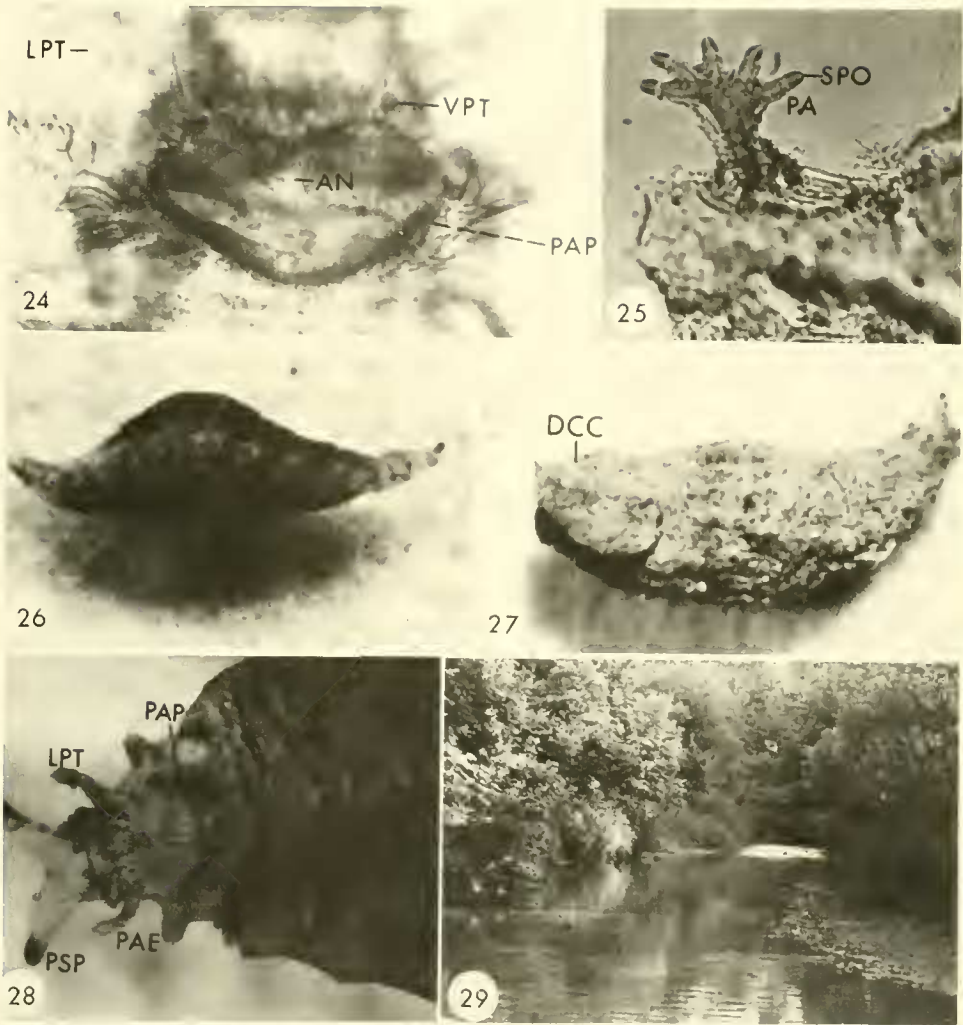
When laboratory colonies of *Parydra* were infested by snails, which feed on the mud, the larvae and the adults of the three fly species died within a few days. Dissections revealed that the guts of these immatures and adults were empty, while immatures and adults in other holding tanks with the same substrate, but without snails, developed and reproduced.

Frequent and heavy precipitation is believed to be a major mortality factor. Heavy precipitation washed the algae off the mud shores and frequent precipitation did not allow the accumulation of an adequate food density on the mud shores. Rising water level due to heavy precipitation diminished the area of exposed mud shores and therefore diminished the feeding areas of the *Parydra*. Possibly most important as a mortality agent of the three species were these effects of heavy precipitation and the resulting large water fluctuations. During heavy rains many eggs and larvae were washed off the mud shores or ended up being covered by shifting substrate when the water level rose drastically.

DESCRIPTIONS OF IMMATURE STAGES

Egg (Fig. 15).—Length with fecal covering 0.61–0.73 mm (\bar{x} = 0.67); length without fecal covering (length of chorion) 0.51–0.60 mm (\bar{x} = 0.52 mm); width 0.16–0.21 mm (\bar{x} = 0.19 mm). Chorion microgranulose, hyaline; newly laid eggs nearly white, elliptical, convex dorsally, nearly flat ventrally (based on 55 specimens laid in the laboratory).

First-instar larva.—Length 0.66–1.8 mm; width 0.1–0.23 mm. First instar similar to third instar except in the following characters (Figs. 16, 19). Furcate structures absent; only 1 pair of suprabuccal teeth apparent. Anterior spiracles absent, with only slight protuberance at their future site. Perianal pad proportionately larger in the first instar; in contrast to *P. quadrituberculata*, postanal elongation relatively longer than in third instar; postanal elongation is about 15 percent of



Figs. 24-29. *Parydra breviceps*. 24, Third-instar larva, perianal pad, 60 \times . 25, Third-instar larva, left anterior spiracle, posterior view, five papillae, 300 \times . 26, Puparium, lateral view, dorsocephalic cap removed, 15 \times . 27, Puparium, dorsal view, covered with substrate debris, dorsocephalic cap opened. 28, Puparium, ventral view of posterior end, 50 \times . 29, Site 2, the mud shore in right side of picture at Harkers Run.

preanal length, whereas in third instar it is 8.7 percent. Posterior spiracles distinctly tapered, proximal end ca. 66 percent wider than distal end, with 2 spiracular orifices (Figs. 10, 21), no spiracular remnant, and 4 spiracular hydrofuge processes. Cephalopharyngeal skeleton (Figs. 5, 6) length (excluding mouthhooks) 0.09-0.13 mm. Pharyngeal sclerite not paler; mouthhooks more pointed and less sharply curved distally and apparently fused basally with ends of dental sclerites; anterior arms of hypostomal sclerite fused, but not in tapering point as in *quadrituberculata*; parastomal bars parallel to hypostomal sclerite, fused anteriorly in a tapering point. Dorsal bridge indistinct; distal parts of dorsal and ventral cornua

and anterior part of cornua next to hypostomal sclerite and parastomal bars light brown, central part of the cornua dark brown.

Second-instar larva.—Length 1.2–2.52 mm; width 0.21–0.5 mm. Similar to third instar except in following characters. In contrast to *quadrituberculata*, setulosity not shorter or paler. Posterior pair of suprabuccal teeth in facial mask proportionately longer and farther apart. Anterior spiracles smaller without real papillae, but just 3 or 4 short buds. Perianal pad less distinctly bilobate. Also in contrast to *quadrituberculata*, postanal elongation relatively longer, about 14 percent of preanal length. Posterior spiracle distinctly tapered, proximal end 66 percent wider than distal end, with 3 orifices and less distinct spiracular remnant (Fig. 9). Cephalopharyngeal skeleton (Figs. 3, 4) length (excluding mouthhooks) 0.15–0.21 mm. Mouthhooks proportionately longer and narrower, somewhat longer than hypostomal sclerite. Ligulate sclerite single, projecting slightly farther anteriorly, and apparently fused basally to shorter, paler epistomal plate. Pharyngeal sclerite with dorsal bridge straplike and directed anterodorsad. No C-shaped recess on ends of dorsal cornua, in contrast to *quadrituberculata* (Deonier and Regensburg, 1978). Ventral length of pharyngeal sclerite 1.9–2.0 times the hypostomal length.

Third-instar larva.—Length 2.3–4.2 mm; width 0.56–0.9 mm. Light gray or creamy white, except light-brown posterior spiracles, setae and spinules (Figs. 19, 20). Densely setulose and spinulose; integument translucent; body slightly depressed and subfusiform, tapering gradually from middle to head-lobe and to anus. Head-lobe, in ventral view of protracted state with 1 pair of conspicuously black-tipped posteriorly directed toothlike sclerites slightly anterior to mouthhooks, but closer together than mouthhooks (Fig. 20). Deonier and Regensburg (1978) mentioned that these sclerites closely resemble suprabuccal teeth shown by Muirhead-Thomson (1937). Anterior to suprabuccal teeth and farther apart, a pair of 2-segmented antennae; segments distinguished by two ring-shaped light-brown sclerites; proximal ring-shaped sclerites of antennae incomplete anteriorly; antennae slightly longer than posterior suprabuccal teeth with terminal segment cylindrical, round and apically and longer than first segment. Prothoracic dorsum with 2 dorsal transverse, irregular rows of sharp, posteriorly-directed spinules, followed by wide zone of minute sharp spinules; center of dorsum of prothorax between antennae with small elliptical area without spinules. Prothoracic venter only sparsely spinulose. Anterior spiracles protrusile, each with 4–6 vertically aligned, digitiform papillae enlarged apically for spiracular orifices (Figs. 23, 25). Mesothoracic dorsum anteriorly with transverse area of medium-sized spinules followed by 3–5 rows of spinules, preceding a wide patch of minute microspinules and microsetulae. Venter with creeping welt consisting of central area with very minute microspinules, surrounded mainly anterolaterally by microspinules and spinules. Metathoracic dorsum with 2–5 irregular anterior transverse rows of spinules. Venter with lateral triangles or spinules followed by elliptical creeping welt. Dorsum of abdominal segment 1 with 3–5 anterior rows of setulae followed by transverse groove without setulae, preceding 2 rows of setulae. Venter of segments 1–8 each with 3 irregularly bi- or triseriate zones of setulae. Dorsum of abdominal segments 2–7 each with 3 irregularly bi- or triseriate zones of setulae with paired lateral and dorsolateral protuberances; all protuberances more or less papilliform or moundlike. Dorsum of abdominal segment 8, anterior to perianal pad with wide microsetulous zone between paired ventrolateral protuberances.

Perianal pad bilobate, protrusile, and posteriorly expansive with paired ventral postanal tubercles (Fig. 24). Postanal elongation of abdominal segment 8 ca. 8.7 percent of preanal length. Posterior spiracles gradually tapered, ca. 66 percent wider at proximal than at distal end (Fig. 22), in distal view (Fig. 8) with 4 ovoid spiracular orifices, each bordered by hydrofuge process consisting of basal attachment piece bearing 4–6 spiculate, sometimes bifurcated uniseriate setulae having, in contrast to *quadrituberculata*, no membranous web between setulae. Ovoid spiracular remnant distinct in distal view. Cephalopharyngeal skeleton (Figs. 1, 2) length (excluding mouthhooks) 0.23–0.3 mm. Pharyngeal sclerite medium to dark brown towards dorsal bridge, on bifurcation, and proximally on cornua, but light brown with brown fibrous streaks towards hyaline borders; other sclerites, except light-brown epistomal plate and piece of hypostomal sclerite next to pharyngeal sclerite and fenestra of mouthhooks, dark brown or black. Mouthhooks separated basally from hypostomal sclerite; mouthhooks slightly shorter than hypostomal sclerite; hook nonserrate and sickle-shaped; base part of mouthhooks conspicuously fenestrate with dorsal condyloid process; base part articulating posterodorsally with anterior arm of hypostomal sclerite and base of dental sclerite. Hypostomal sclerite, in ventral view, narrowing anteriorly, with hypostomal bridge located $\frac{1}{4}$ of distance from posterior end and ventral to posterior margin of shield-shaped epistomal plate. Pharyngeal and hypostomal sclerites not fused. Dorsal bridge convex and steeply angled posterodorsally. Dorsal cornua ending in partial C-shaped recess; anteroventral arm of recess with small angulate process; ventral cornua narrowing at midlength and, in contrast to *quadrituberculata*, ending in single arm. Ventral length of pharyngeal sclerite 2.2–2.5 times length of hypostomal sclerite.

Puparium.—Length 3.7–4.55 mm; width 1.1–1.4 mm. Postanal elongation 13.7 percent of preanal length. Empty puparium opaque and medium to dark brown. In contrast to *quadrituberculata*, not steeply upturned, often almost straight (Fig. 26). Venter of preanal portion straight with upturn at anterior end; dorsum strongly arched to anterior end and posteriorly towards postanal elongation. Anterior spiracles light to medium brown, borne anterolaterally on dorsocephalic cap with truncated anterior and undulant posterior margin. Cap with zones of microspinules between the dorsal parts of 2 anterior bands having 2–5 irregular rows of spinules and 2 posterior bands having, respectively, 3–5 and 2–3 irregular rows of setulae. Puparium with only slightly elevated protuberances (Figs. 26, 27) and like *quadrituberculata* with 18 more or less encircling irregularly bi- or triseriate bands of setulae between dorsocephalic cap and anterior edge of the remnant of perianal pad (in *quadrituberculata* perianal pad); with 1 more or less encircling, irregularly triseriate band of setulae and 1 wider encircling zone of setulae posterior to perianal pad. Most empty puparia dark brown to anterior edge of remnant of perianal pad and light brown from there to posterior spiracles. Remnant of perianal pad without ventral postanal tubercles. Postanal elongation very short in comparison to *quadrituberculata*. Spiracular orifices and hydrofuge processes same as in third instar; spiracular remnant much wider than in third instar.

LITERATURE CITED

- Becker, T. 1926. Ephyridae (Fam. 56), pp. 1–115. In Lindner, E., ed., Die Fliegen der Palaearktischen Region 6, pt. 1. Stuttgart.

- Bohart, G. E. and J. L. Gressitt. 1951. Filth-inhabiting flies of Guam. Bull. Bernice P. Bishop Mus. 204: 1-152.
- Clausen, P. J. and E. F. Cook. 1971. A revision of the Nearctic species of the tribe Parydrini (Diptera: Ephydriidae). Mem. Am. Entomol. Soc. 27: 1-150.
- Deonier, D. L. 1971. A systematic and ecological study of Nearctic *Hydrellia* (Diptera: Ephydriidae). Smithson. Contr. Zool. 68: 1-147.
- . 1972. Observations on mating, oviposition, and food habits of certain shore flies (Diptera: Ephydriidae). Ohio J. Sci. 72: 22-9.
- Deonier, D. L. and J. T. Regensburg. 1978. Biology and immature stages *Parydra quadrutuberculata* (Diptera: Ephydriidae). Ann. Entomol. Soc. Am. 71: 341-353.
- Frey, R. 1921. Studien über den Bau des Mundes der niederen Diptera Schizophora nebst Bemerkungen über die Systematik dieser Dipteregruppe. Acta Soc. Fauna Flora Fenn. 48: 1-245, 10 pls.
- Meyers, D. M. 1981. A behavioral-ecological study of *Kleidotoma* sp. (Hymenoptera: Eucolidae), with notes on *Anaphes* sp. (Hymenoptera: Mymaridae). M. S. Thesis. Miami University, Oxford, Ohio.
- Muirhead-Thomson, R. C. 1937. Observations on the biology and larvae of the Anthomyiidae. Parasitology. 29: 273-58.
- Reeder, W. G. 1951. Stomach analysis of a group of shorebirds. Condor 53: 43-5.
- Thier, R. W., R. S. Zack, and B. A. Foote. 1976. *Anaphes* (Hymenoptera: Mymaridae) reared from the eggs of a shore fly (Diptera: Ephydriidae). Great Lakes Entomol. 9: 205-6.
- Thier, R. W. and B. A. Foote. 1980. Biology of mud-shore Ephydriidae (Diptera). Proc. Entomol. Soc. Wash. 82: 517-535.
- Thorpe, W. H. 1930. The biology of the petroleum fly (*Psilopa petrolei*, Coq.). Trans. R. Entomol. Soc. Lond. 78: 331-34.
- Wirth, W. W. 1971. *Platygyrnopa*, a new genus of Ephydriidae reared from decaying snails in North America (Diptera). Can. Entomol. 103: 266-70.